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BY

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THE ALTERNATE HOSTS OF CROWN RUST, PUCCINIA CORONATA CORDA[1]

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INTRODUCTION

As has been shown previously (*9*, *4*),[3] many species of the genus Rhamnus are susceptible to crown rust (*Puccinia coronata* Corda) and play an important rôle in the dissemination of this disease in America. The universal presence of the uredinial stage of this rust in certain regions where no Rhamnus is found or only resistant species occur led the writer to a further study of the range of the aecial hosts of this fungus.

European investigators have been interested in the alternate hosts of crown rust since 1866 when De Bary (*3*) discovered that *Rhamnus cathartica* L. harbored the aecial stage. An earlier résumé (*9*) of the literature on the alternate hosts of *Puccinia coronata* and their ability to spread rust in the open (*4*) makes unnecessary a review in this paper.

The reaction of 16 species and 1 variety of Rhamnus to crown rust, the testing of 4 genera other than Rhamnus, and the determination of the rôle of *R. cathartica* L. and *R. lanceolata* Pursh. in initiating local and general epidemics of *Puccinia coronata* in the upper Mississippi Valley are considered in this paper.

MATERIALS AND METHODS

During the past six years studies have been made in the greenhouse and laboratories of the Iowa Agricultural Experiment Station at Ames, Iowa, to determine the reaction of 16 species and 1 variety of Rhamnus, and 5 species of 4 other genera, to crown rust. Succulent young leaves were inoculated with germinating teliospores from *Avena sativa* L., *Calamagrostis canadensis* (Michx.) Beauv., *C. purpurascens* R. Br., *Festuca elatior* L., and *Notholcus lanatus* (L.) Nash. (*Holcus lanatus* L.). The species of Rhamnus and other genera were exposed to infection by placing them in a moist chamber with teliospore-laden straw. The plants, straw, and sides of the chamber were then wet by a fine spray. In cases where scant spore material was available, the spores were germinated on the straw in Petri dishes as described by Melhus and Durrell (*8*). Later, the sporidia were washed off and sprayed onto the plants with an atomizer. If the chamber showed signs of becoming dry before the close of the incubation period, it was opened and sprayed again. This

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[2] The writer wishes to express to I. E. Melhus, J. C. Gilman, and H. B. Humphrey his appreciation for much assistance in the preparation of the manuscript, and to the last named also his thanks for the collection of the field data on *Rhamnus frangula* L.

[3] Reference is made by number (italic) to "Literature cited." p. 969.

method successfully induced infection. At the end of two days the plants were removed to the greenhouse bench, where they were observed for the appearance of rust.

SOURCE AND CARE OF ALTERNATE HOSTS

Five additional native and two European species of Rhamnus have become available for alternate-host studies since 1922. Species of Ceanothus, Berchemia, and Zizyphus, of the family Rhamnaceae, together with two species of Lepargyrea, of the family Eleagnaceae, have been studied to determine their reaction to germinating teliospores of *Puccinia coronata*.

Rhamnus dahurica Pallas is a cultivated shrub indigenous to the territory between India and northern Asia. Its bark is used in the manufacture of Chinese green indigo. Because of its extreme hardiness, this shrub is becoming common for landscaping in certain sections of America where the winters are severe. The material used here was grown from seed collected on the campus at Ames, Iowa.

Rhamnus ilicifolia Kellogg is native to southern and middle California, and is especially abundant on Angel Island, in San Francisco Bay, where it often reaches a height of 10 to 12 feet. It is very similar to *R. crocea*, but differs from the latter in its arboreous habit, gray bark, and larger leaves and fruit. This material was obtained in California.

Rhamnus nevadensis Nelson is indigenous to Nevada. It is very similar to *R. californica* Esch., but has noncoriaceous leaves and short calyx lobes. It seems much hardier under Iowa conditions. The one plant available in this investigation was found in Nevada.

Rhamnus pachyphylla Heller, native to California, has a limited distribution. Its leaf is thick and leathery with an entire margin. *R. pinetorum* Heller also has a rather limited distribution in California.

Rhamnus rubra Greene is listed by Trelease (*14*) as a variety of *R. californica*. Greene (*6, p. 160*), however, thinks it a good species, since its seeds are only half as large as those of *R. californica* and also are decidedly narrowed at the base. The plants used in these experiments had bark of a deeper red than those of *R. californica*. This species is common in California, especially in Butte County between Upper Soda Springs and Shasta Retreat. The writer is indebted to A. A. Heller for the collection of *R. pachyphylla*, *R. pinetorum*, and *R. californica*.

Rhamnus tinctoria Waldst. and Kit. is native to Europe and Asia Minor, where it is used in the manufacture of dye.

Berchemia scandens (Hill) Trel. is a climbing plant growing in damp soils from Virginia to Missouri and southward. The stems are tough and lithe, hence the popular name, supple-jack. This material was collected in southern Alabama.

Ceanothus americanus L., commonly called New Jersey tea, grows in dry woodlands, along gravelly shores and sandy knolls, from central Maine to western Ontario and southward through Iowa. The material employed in these studies was collected 3 miles north of Ames, Iowa, on virgin prairie land.

Lepargyrea argentea Greene is widely distributed in the northeastern part of the United States and Canada, extending southward

to northern New Mexico in the Rocky Mountain region. *L. canadensis* Greene is even more extensive in distribution than *L. argentea.* It extends across southern Canada and up to Alaska. In the Rocky Mountain region, however, temperature seems to limit its southern distribution, as this shrub could be found only at an elevation in excess of 7,500 feet near Bergen Park, in Colorado. The materials used in these investigations were collected at Pagosa Spring and Bergen Park, Colo.

Zizyphus lycioides Gray, a spiny shrub with zigzag branches, is native to the southern part of the United States. The material used was collected in southern Alabama.

Considerable difficulty was experienced at first in overwintering these plants. As an extremely succulent growth was needed for inoculation during six weeks in the spring, the question arose as to the best method of maintaining these plants throughout the remainder of the year. Four methods, all unsatisfactory at Ames, were as follows: (1) Maintenance under greenhouse conditions throughout the year; (2) heeling-in during the winter out of doors and transferring to the greenhouse in the spring; (3) packing in moss and keeping in cold storage during the winter; (4) cuttings.

Two methods of obtaining succulent spring growth were successfully used at Ames. In the first, the plants were set in 12-inch pots placed outdoors in June, and set 3 inches below the ground line. They were allowed to harden off in the fall until defoliated, after which they were covered with 6 inches of straw and allowed to remain outside until the first of March. They were then kept in a cold room (45° to 55° F.) for three weeks and subsequently placed on the greenhouse bench (temperature 65° to 70°). It seems important that these plants be started slowly when brought into the greenhouse, as in previous years over 50 per cent of them died when taken directly from the outside into a heated room.

A second satisfactory method was to sow Rhamnus seed in the greenhouse in November. Seeds of *R. dahurica, R. lanceolata, R. cathartica, R. californica, R. purshiana,* and *R. alnifolia* germinated strongly if gathered in the fall and sown before the fruit became dry.

After the plants had become established on the greenhouse bench in the spring, two methods of obtaining succulent growth were used: (1) The plants were watered daily with liquid manure and the temperature raised to 75° to 80° F.; (2) the seedlings, which had been maintained under greenhouse conditions, were severely pruned and then forced by means of fertilizer and heat.

SOURCE AND CARE OF TELIOSPORES

During 1923, teliospores from *Avena sativa* L. were collected from four places in Iowa and Illinois. These had a low percentage of germination. Those collected at Ames and Masonville, Iowa, during 1924, germinated with greater vigor.

Teliospores were collected from *Calamagrostis canadensis* in Iowa, Wisconsin, and Canada. Those from Iowa germinated between 90 and 100 per cent, but the other collections had only a weak germination. Teliospores were collected at Eldora Springs, Colo., from *C. purpurascens.*

A collection of teliospores from *Festuca elatior* was made at Ames, Iowa. Teliospores were collected from greenhouse cultures of *Notholcus lanatus* but germinated poorly.

The germination of teliospores in the spring was influenced by the method of overwintering the host plants. Those from *Avena sativa*, *Festuca elatior*, and *Notholcus lanatus* germinated most satisfactorily when the host plant was left in the field and the spore material collected in the spring, while those on *Calamagrostis canadensis* germinated equally well whether collected in the fall and wrapped in cheesecloth or obtained from the host plant in the spring.

TYPES OF INFECTION OF ALTERNATE HOSTS

Successful attempts to infect Rhamnus species developed the following four types of aecial infection: (1) Necrotic areas, no sporulation; (2) normal pycnia, no aecia; (3) normal pycnia, and few aecia; (4) normal pycnia and aecia.

In type 1 the germ tube of the sporidium caused etiolated, light yellow areas, usually surrounding a dead center with no form of sporulation. In type 2, there was normal pycnial development but little or no evidence of aecia. Type 3 showed normal pycnia but few aecia. Type 4 was characterized by profuse development of normal pycnia and aecia.

Growth factors, such as relative humidity and temperature, played an important part in determining whether an infection of type 3 or 4 would develop. A high humidity and a temperature of about 20° C. caused profuse development of aecial cups on susceptible Rhamnus species. Inherent rather than environmental causes were probably more responsible in determining whether aecial infection was of type 2 or 3.

THE ALTERNATE HOSTS OF CROWN RUST

It has been shown earlier (*9*) that the uredinial hosts of *Puccinia coronata* are not restricted to one genus. Whether the alternate host of crown rust was limited to the genus Rhamnus has not previously been known. To determine this, the following genera were exposed to infection from teliospores of crown rust: Berchemia, Ceanothus, Leparagyrea, Rhamnus, and Zizyphus.

THE GENUS RHAMNUS

The results obtained by exposing 16 species and 1 variety of Rhamnus to crown-rust infection 364 times are presented in Table 1. Teliospores from *Avena sativa*, *Calamagrostis canadensis*, and *Festuca elatior* were used, as these gramineous hosts are generally present throughout the main oat-growing sections of the upper Mississippi Valley.

TABLE 1.—*Response of Rhamnus species to inoculation with teliospores of Puccinia coronata from various grasses, in the years 1919 to 1924, inclusive*

Rhamnus species	Teliospores from—	Times inoculated	Types of infection				
			None	Flecks	Pycnia	Few aecia	Normal
Alnifolia	Avena sativa	12	7	1		4	
Do	Calamagrostis canadensis	15	2	1			12
Do	Festuca elatior	2	1				1
Californica	Avena sativa	13	4			9	
Do	Calamagrostis canadensis	18	1	1	7	8	1
Do	Festuca elatior	4	2		1		1
Californica var. tomentella.	Avena sativa	7	2			2	3
Do	Calamagrostis canadensis	13	3	4	6		
Do	Festuca elatior	4	2		2		
Caroliniana	Avena sativa	13	7		3	1	2
Do	Calamagrostis canadensis	11	5	2	4		
Do	Festuca elatior	2				2	
Cathartica	Avena sativa	26	2				24
Do	Calamagrostis canadensis	24	14	5	3	2	
Do	Festuca elatior	5					5
Crocea	Avena sativa	1				1	
Do	Calamagrostis canadensis	6					6
Do	Festuca elatior	1				1	
Dahurica	Avena sativa	13	5	1	3	4	
Do	Calamagrostis canadensis	6	5		1		
Do	Festuca elatior	2	2				
Frangula	Avena sativa	17	8	7	2		
Do	Calamagrostis canadensis	28	23	3	2		
Do	Festuca elatior	3	3				
Ilicifolia	Avena sativa	4	2				2
Do	Calamagrostis canadensis	3	3				
Do	Festuca elatior	1		1			
Lanceolata	Avena sativa	11	2				9
Do	Calamagrostis canadensis	24	5	1		4	14
Do	Festuca elatior	3					3
Nevadensis	Avena sativa	1	1				
Do	Calamagrostis canadensis	0					
Do	Festuca elatior	0					
Pachyphylla	Avena sativa	5	1		3		1
Do	Calamagrostis canadensis	4			4		
Do	Festuca elatior	1		1			
Pinetorum	Avena sativa	3	1				2
Do	Calamagrostis canadensis	2				2	
Do	Festuca elatior	1	1				
Purshiana	Avena sativa	8	3	3	2		
Do	Calamagrostis canadensis	10	7	2	1		
Do	Festuca elatior	3	3				
Rubra	Avena sativa	5				4	1
Do	Calamagrostis canadensis	6				6	
Do	Festuca elatior	2	1			1	
Smithii	Avena sativa	7	1			2	4
Do	Calamagrostis canadensis	10	1				9
Do	Festuca elatior	1				1	
Tinctoria	Avena sativa	1				1	
Do	Calamagrostis canadensis	1			1		
Do	Festuca elatior	1	1				

When inoculated with teliospores from *Avena sativa*, it was found that *Rhamnus californica* var. *tomentella*, *R. caroliniana*, *R. cathartica*, *R. ilicifolia*, *R. lanceolata*, *R. pachyphylla*, *R. pinetorum*, *R. rubra*, and *R. smithii* were susceptible, producing type-4 infection, and that *R. alnifolia*, *R. californica*, *R. crocea*, *R. dahurica*, and *R. tinctoria* produced a type-3 infection (figs. 1 and 2). *R. frangula*, *R. nevadensis*, and *R. purshiana* showed a marked resistance to this physiologic form of rust. *R. dahurica* probably possesses inherent resistance (fig. 2), as the aecial sori were small, and contained only a few cluster cups. More inoculations are necessary to determine the true response of *R. nevadensis*, as only one plant was available in the experiments here recorded. When inoculated with teliospores from *Calamagrostis canadensis*, *R. alnifolia*, *R. californica*, *R. crocea*, *R. lanceolata*, and *R.*

smithii were infected normally. In addition, *R. cathartica*, *R. pinetorum*, and *R. rubra* may function as alternate hosts for this form, as they produced a type-3 infection. The other eight species of Rhamnus showed a marked resistance.

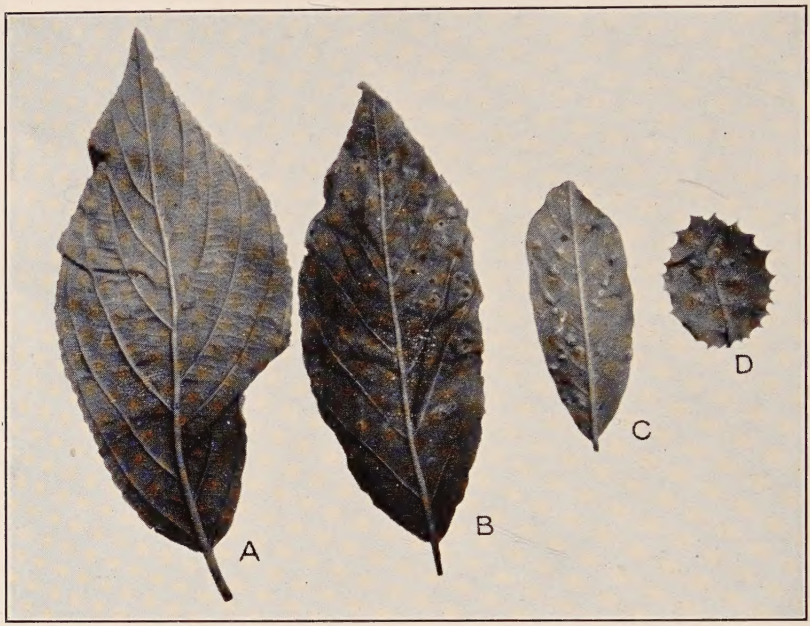

FIG. 1.—Infection from *Avena sativa* on Rhamnus species. A, *Rhamnus alnifolia;* B, *R. caroliniana;* C, *R. rubra;* D, *R. ilicifolia*

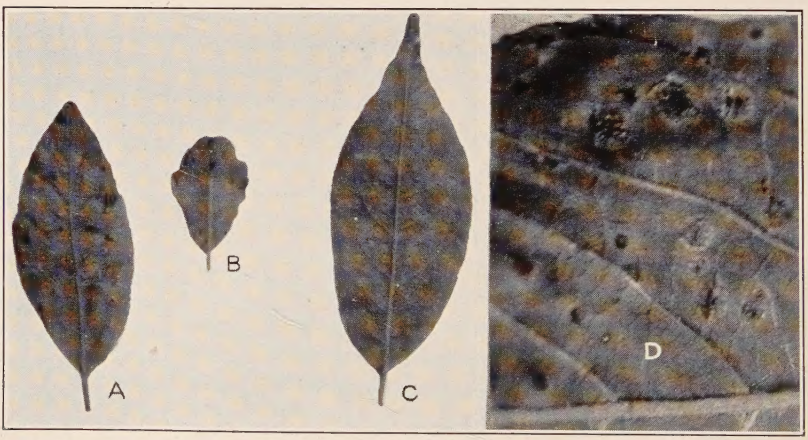

FIG. 2.—Infection from *Avena sativa* to Rhamnaceae. A, *Rhamnus smithii;* B, *R. pinetorum;* C, *R. lanceolata;* D, *R. dahurica.* × 3

Teliospores from *Festuca elatior* caused normal infection on *Rhamnus alnifolia*, *R. californica*, *R. cathartica*, and *R. lanceolata*. On *R. caroliniana*, *R. crocea*, *R. rubra*, and *R. smithii* a few aecia were produced. Twelve inoculation trials on the seven remaining Rhamnus species

showed that *R. ilicifolia* produced pycnia and *R. pachyphylla* became flecked. Owing to the limited teliospore material, further investigation is necessary to determine the reponse of Rhamnus species to crown rust from *F. elatior*.

A limited inoculum of teliospores from *Notholcus lanatus* was transferred to *Rhamnus alnifolia*, *R. californica*, *R. californica* var. *tomentella*, *R. cathartica*, *R. caroliniana*, *R. crocea*, *R. frangula*, *R. lanceolata*, *R. purshiana*, and *R. smithii*. *R. lanceolata* produced pycnia. Further tests are necessary.

It should be noted that the reaction of the Rhamnus species to crown rust from *Festuca elatior* paralleled closely that resulting from the strain from *Avena sativa*. A greater divergence between the reaction of the *A. sativa* and *Calamagrostis canadensis* strains is apparent. The reaction of *R. caroliniana* to the strain from *A. sativa* is particularly noticeable, as this species was infected normally but twice in 13 attempts. The normal infection occurred during 1924, the most favorable year for obtaining infection in the six years of experimentation. Although *R. frangula* was inoculated 48 times and *R. purshiana* 21 times, both maintained a marked resistance to crown rust from the three gramineous hosts.

Many of the Rhamnus species contained some individuals which showed no infection and others which showed normal infection (Table 1). This variation probably was not always due to an inherent difference in the individuals, as some of the same plants developed no infection at one inoculation and normal infection during a subsequent attempt. The species were divided into susceptible and resistant groups. All that functioned as alternate hosts by producing aecia were classified as susceptible.

TABLE 2.—*Division of Rhamnus species into susceptible and resistant groups according to types of infection*

Inoculated with teliospores from—	Susceptible species							Resistant species						
	Number of species	Number of trials	Types of infection					Number of species	Number of trials	Types of infection				
			None	Flecks	Pycnia	Few aecia	Normal			None	Flecks	Pycnia	Few aecia	Normal
Avena sativa	14	121	34	2	9	28	48	3	26	12	10	4	0	0
Calamagrostis canadensis	[a]9	108	26	12	10	28	32	[a]7	63	43	7	13	0	0
Festuca elatior	[a]9	24	6	0	1	7	10	[a]7	12	10	1	1	0	0
Total	----	253	66	14	20	63	90	----	101	65	18	18	0	0

[a] *Rhamnus nevadensis* was exposed to infection only with teliospores from *Avena sativa*.

The production of a single aecium was considered indicative of the inherent susceptibility of a species, and when further trials produced only negative results it was held to be due probably to the environmental conditions of the plant during inoculation or to possible nonviability of the teliospores. As shown in Table 2, the mode of each dispersion is at the normal class when inoculations were made with spores from *Avena sativa*, *Calamagrostis canadensis*, or *Festuca*

elatior, respectively. A total of 253 inoculations of the species classified as susceptible resulted in 187 positive and 66 negative reactions; 63 developed a few aecia. Ninety of the 187 positive reactions were of normal type.

Those species were classed as resistant which did not function as alternate hosts; that is, those which produced only a maximum development of pycnia, or produced only flecks, or no infections. In this class, 65 of a total of 101 inoculations, or over 64 per cent, were negative. It is obvious that it is increasingly more difficult to secure infection in the resistant than the susceptible class, a condition due probably to the inherent resistance of certain species of Rhamnus.

The maximum degree of infection obtained at any time on each species of Rhamnus is recorded in Table 3. As the importance of any Rhamnus species as an alternate host may depend on its degree of susceptibility under optimum conditions, the maximum degree of infection serves as an index of the possible danger from each particular species. Crown rust obtained from all of the three telial hosts developed aecia on *R. alnifolia*, *R. californica*, *R. californica* var. *tomentella*, *R. cathartica*, *R. crocea*, *R. lanceolata*, *R. rubra*, and *R. smithii*.

TABLE 3.—*Maximum infection on Rhamnus species, expressed in types of infection 1 to 4, after inoculation with teliospores from three grasses during the period 1919 to 1925, inclusive*

Inoculated with teliospores from—	R. alnifolia	R. californica	R. californica tomentella	R. caroliniana	R. cathartica	R. crocea	R. dahurica	R. frangula	R. ilicifolia	R. lanceolata	R. nevadensis	R. pachyphylla	R. pinetorum	R. purshiana	R. rubra	R. smithii	R. tinctoria
Avena sativa	3	3	4	4	4	3	3	2	4	4	[a]0	4	4	2	4	4	3
Calamagrostis canadensis	4	4	3	2	3	4	2	2	0	4	----	2	3	2	3	4	2
Festuca elatior	4	4	3	3	4	3	0	0	1	4	----	1	0	0	3	3	0

[a] 0 = no infection.

Figure 3 represents those species of Rhamnus which may function as alternate hosts for the physiologic forms of crown rust on *Avena sativa*, *Calamagrostis canadensis*, or *Festuca elatior*.

OTHER GENERA

Other genera of Rhamnaceae and Eleagnaceae were studied as alternate hosts of crown rust. The late Ellsworth Bethel, of Denver, Colo., found *Lepargyrea canadensis* and *L. argentea* bearing aecia when growing near gramineous hosts of crown rust. Arthur (*1*) exposed these two shrubs to teliospores from *Notholcus lanatus* and *Scolochloa festucacea* but obtained no infection.

Lepargyrea canadensis, *L. argentea*, *Ceanothus americanus*, *Berchemia scandens*, and *Zizyphus lycioides* were inoculated in 1921 with teliospores from *Avena sativa*, *Calamagrostis canadensis*, *C. purpurascens*, and *Festuca elatior* (Table 4). On *L. canadensis*, inoculated with teliospores from *C purpurascens*, a heavy normal infection developed (fig. 4). All other results with this gramineous host were negative. The results on Lepargyrea were verified by cultures grown under controlled conditions at Denver, Colo., by I. W. Clokey during the summer of 1922. Unfortunately, no teliospores were available in 1923 with which to inoculate Ceanothus, Berchemia, and Zizyphus.

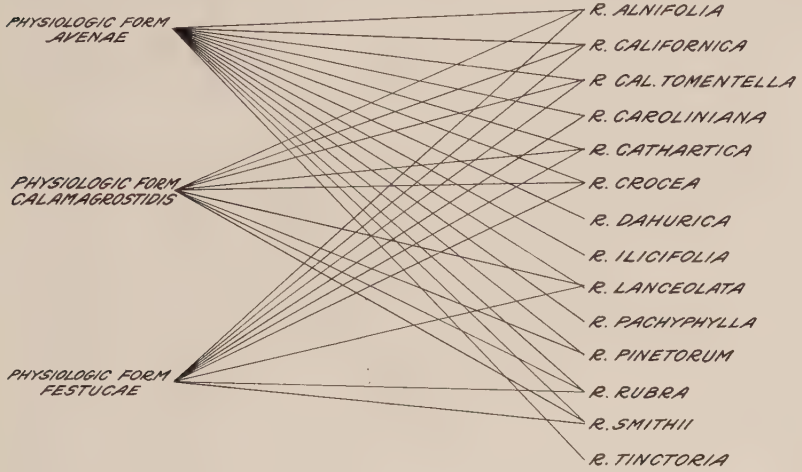

FIG. 3.—Diagrammatic representation of the alternate hosts of three physiologic forms of *Puccinia coronata*

TABLE 4.—*Reaction to Puccinia coronata of species in genera other than Rhamnus*

Inoculated with teliospores from—	Species inoculated					
	Number of inoculations on each species	Lepargyrea argentea	Lepargyrea canadensis	Ceanothus americanus	Berchemia scandens	Zizyphus lycioides
Avena sativa	3	0	0	0	+	0
Calamagrostis canadensis	3	0	0	0	0	0
Calamagrostis purpurascens	4	0	+	−	−	−
Festuca elatior	2	0	0	0	0	0

0 = no infection + = infection. − = not tried.

In July, 1924, aecia were collected on *Lepargyrea canadensis* near Bergen Park, Colo., and aeciospores from these were transferred to *Avena sativa* at Ames, Iowa. Although urediniospores were produced on oats, the results are not conclusive because the aecia were not produced under controlled conditions. *L. argentea* is listed by Arthur (*2, p. 313*) as an alternate host of crown rust, but the writer was unable to obtain infection through inoculation with teliospores from *A. sativa*, *Calamagrostis canadensis*, *C. purpurascens*, or *Festuca elatior*, at Ames, Iowa.

Berchemia scandens was inoculated on May 5, 1924, with teliospores from *Avena sativa*. By May 19, pycnia had developed and two days later a few aecia were noted. This experiment was repeated, and four inoculated plants produced a few aecia. *B. scandens* may function as an alternate host for *Puccinia coronata*, although it shows some degree of resistance, as indicated by the small aecia with few cups.

FIG. 4.—*Lepargyrea canadensis* showing aecia after inoculation with teliospores from *Calamagrostis purpurascens*

THE EFFECT OF RHAMNUS SPECIES ON PHYSIOLOGIC FORMS OF P. CORONATA

As a heteroecious rust like *Puccinia coronata* completes its life cycle on two widely different plants, the question of the possible effect of the alternate host on the biology of the parasite frequently has arisen. Whether the alternate host stimulates or invigorates the fungus in some manner, or changes its biologic response, has not been known. Some light is thrown on the latter phase in this paper.

The range of gramineous hosts of the physiologic forms of crown rust has been previously reported (*9*). In an earlier report (*9*) and in the present paper, the reaction of 16 Rhamnus species to crown rust is recorded. In order to complete the chain of evidence, the range of gramineous hosts of the aeciospores from Rhamnus should be determined.

Inoculating with teliospores from *Avena sativa*, aecial infection was secured on *Rhamnus caroliniana*, *R. cathartica*, *R. dahurica*, *R. ilicifolia*, *R. lanceolata*, *R. pinetorum*, *R. rubra*, and *R. smithii*. *Achyrodes aureum*, *Avena sativa*, *Calamagrostis canadensis*, *Festuca elatior*, and *Notholcus lanatus* were inoculated with aeciospores from each infected species of Rhamnus. Aeciospores from all eight Rhamnus species caused infection on *Avena sativa*. All results are shown in Table 5.

TABLE 5.—*Gramineous host range of Puccinia coronata avenae, determined by inoculation with aeciospores from eight Rhamnus species*

Species	Gramineous hosts				
	Achyrodes aureum	Avena sativa	Calamagrostis canadensis	Festuca elatior	Notholcus lanatus
R. caroliniana	+[a]	+			+
R. cathartica	+	+		+	+
R. dahurica		+			
R. ilicifolia		+	+	+	
R. lanceolata	+	+	+	+	+
R. pinetorum		+			+
R. rubra	+	+			+
R. smithii		+			+

[a] +=infection.

In some cases, the number of aeciospores was limited; hence the negative results of Table 5 are not conclusive. This was true particularly of *Rhamnus dahurica*, *R. ilicifolia*, and *R. pinetorum*. Inoculum from *R. caroliniana*, *R. cathartica*, *R. lanceolata*, *R. pinetorum*, *R. rubra*, and *R. smithii* produced urediniospores on *Notholcus lanatus*. Urediniospores were produced on *Calamagrostis canadensis* inoculated with aeciospores from *R. ilicifolia* and *R. lanceolata*. *Achyrodes aureum* has been shown to be a host for five physiologic forms of *Puccinia coronata*, two physiologic forms of *P. graminis* and *P. dispersa*, *P. montanensis*, and *P. poarum*. Urediniospores were produced on this grass through inoculation with aeciospores from *R. caroliniana*, *R. cathartica*, *R. lanceolata*, and *R. rubra*.

Rhamnus lanceolata, which had been inoculated with teliospores from *Calamagrostis canadensis*, produced abundant urediniospores on *Avena sativa* in nine trials conducted over a period of three years.

CORRELATION OF LABORATORY AND FIELD RESULTS

Although Rhamnus species may become infected with crown rust under greenhouse conditions, the importance of the alternate hosts of this rust depends on such factors as prevalence and distribution of the species, the quantity of infection, together with the methods of infection, rate of dissemination of their aeciospores, and the resulting damage to the oat crop.

RHAMNUS CATHARTICA IN THE UPPER MISSISSIPPI VALLEY

Through the cooperation of the State leaders of barberry eradication and their field assistants with the plant pathology section of the Iowa Experiment Station, a preliminary survey for the locations of common buckthorn (*Rhamnus cathartica*) was made. In representative areas, comprising less than one-twentieth of the total area in each of the eight upper Mississippi Valley States, a total of 1,021 plantings of *R. cathartica* was found during 1923 and 1924. Of these plantings, 282 were rural and 739 urban. They contained 93,041 counted bushes besides 44,395 feet of hedge where the bushes were not counted. Many wild areas of escaped bushes found in Illinois, Wisconsin, and Montana were not included in this count, for the bushes were too numerous to estimate.

It readily can be seen that with this tremendously large number of shrubs in a relatively small area, a serious, though local, annual damage to the oat crop may result if these shrubs become infected. Since the aecial infection affecting the oat crop could function only a short time in the spring, the percentage of bushes infected was tabulated for the months of May and June, 1923. Nearly 80 per cent of all bushes reported during this period were infected, while those reported from the farmsteads were uniformly infected. In 1924, about 50 per cent of the bushes located during this period were infected. For the past nine years, under Iowa conditions, aecial infection of *Puccinia coronata* developed on *Rhamnus cathartica* and *R. lanceolata* before uredinia were present on *Avena sativa* (Table 6).

TABLE 6.—*Time of appearance of crown-rust uredinia on Avena sativa and aecia on Rhamnus cathartica and R. lanceolata in Iowa for the period 1916 to 1924, inclusive*

Stage in life cycle	Host	Year				
		1916	1917	1918	1919	1920
Aecial	Rhamnus cathartica	May 7	June 30	Apr. 30	May 26	May 15
Aecial	Rhamnus lanceolata	May 22		June 6	May 15	May 20
Uredinial	Avena sativa	June 2	July 6	July 6	June 6	June 12

Stage in life cycle	Host	Year			
		1921	1922	1923	1924
Aecial	Rhamnus cathartica	May 16	May 14	May 21	May 28
Aecial	Rhamnus lanceolata	May 16	May 21	May 23	May 7
Uredinial	Avena sativa	May 22	June 14	June 16	June 16

The earliest appearance of aecia during this period was found on *Rhamnus cathartica* on April 30, and the latest on June 30. The time of the appearance of infection depends somewhat on climatic factors, especially moisture and temperature. *R. lanceolata* varied in time of observed infection from May 7 to June 6. Uredinia usually appear on oats about seven days after visible outbreak of the disease on the alternate host. However, this period was increased greatly in 1918 by the hot, dry weather intervening between aecial and uredinial infection.

In order to prove further that buckthorn was responsible for the initial infection in Iowa, a detailed survey of the State was made during May and June, 1923 and 1924. If wind-blown spores from the south started the infection in Iowa, a more or less uniform rust spread should have appeared first across the southern part of the State. However, during this time, many local areas or concentric zones of crown-rust infection of oats were observed scattered over the State previous to a general infection. Either *Rhamnus cathartica* or *R. lanceolata* was found near the center of each of these areas. The degree of infection varied from a trace on the outer edge of these concentric zones to 30 per cent near the center. These local infection centers appeared simultaneously in northern and southern Iowa. The areas were small at first, remained constant for 7 to 10 days, and then expanded rapidly. This probably was due partly to the limited area over which aeciospores cause infection (*4*). It is probable that infection from rural plantings of Rhamnus is more likely to spread than that from city plantings. This belief is supported by the fact that the centers of all these local infection areas were on farmsteads.

A detailed study of the effect of crown rust on yield was made at Winthrop in Buchanan County, Iowa, where the initial infection was a hedge of *Rhamnus cathartica* adjoining an oat field. The oats were not cut, as many of the plants failed to head. Oats in adjoining sections yielded 10 bushels per acre, while the average yield of more remote sections of the same township was 50 bushels per acre.

RHAMNUS FRANGULA

As previously stated, the maximum infection on *Rhamnus frangula* under controlled conditions gave only pycnia production in 4 out of 48 trials. It seemed desirable to ascertain whether the species maintained this relative resistance under field conditions. During 1923 and 1924, ten plantings or thickets of *R. frangula* in the New England States, ranging from a few to more than 2,000 bushes were inspected for aecial infection. In four of these cases, where *R. frangula* and *R. cathartica* were growing side by side, and often interwoven, aecial infection was found abundantly on *R. cathartica* but was absent on *R. frangula*. Likewise no aecia were found on the other six plantings of *R. frangula*. *R. frangula* bushes, growing on the campus at Ames, Iowa, have produced no aecia during the past eight years of observation, while adjoining bushes of *R. cathartica* were infected annually.

RHAMNUS PURSHIANA

Under controlled conditions, *Rhamnus purshiana*, like *R. frangula*, proved resistant to crown rust. It is a well-known fact that this species produces abundant aecia under natural conditions, although

it remains to be discovered just what, if any, relationship this aecial infection bears to *Puccinia coronata* on *Avena sativa*.

In June, 1922, at New Amsterdam, B. C., the late Ellsworth Bethel succeeded in infecting *Calamagrostis* sp. by inoculating with aeciospores taken from *Rhamnus purshiana* grown in the open.

DISCUSSION

In Europe, crown rust (*Puccinia coronata*) has been divided by Klebahn (*7*) into two species, *P. coronata* and *P. coronifera*. Eriksson (*5*) and Mühlethaler (*10*) are in agreement with Klebahn that *Rhamnus frangula* acts as a differential host for *P. coronata* and *P. coronifera*. Eriksson (*5*) recognizes Barclay's *P. coronata* var. *himalensis* as still further distinct, since it produces aecia on *R. dahurica*. Dietel makes a valid species of this form, and Mühlethaler (*11*) recognizes it, but suggests that it may be *P. coronifera*. These investigators, then, have employed the several species of Rhamnus as indicators of different species of rust. In other words, strong emphasis has been placed on the physiologic reaction of the alternate host. Treboux (*12*), on the other hand, fails to find the marked differential reaction of Rhamnus species reported by Klebahn (*7*), Eriksson (*5*) and Mühlethaler (*11*).

Still further, here in America, Melhus, Dietz, and Willey (*9*) have presented infection experiments suggesting lack of marked differential action of *Rhamnus cathartica* and *R. frangula*. They found that teliospores from *Avena sativa* produced pycnia on *R. frangula* and that the 10 species considered by them showed different degrees of susceptibility ranging from flecking to the normal production of aecia. This varied host behavior led these authors to question the wisdom of founding a species of Puccinia on the basis of its alternate-host reaction.

In these further studies, comprising inoculation trials extending over four years and involving 16 species of Rhamnus, a wealth of additional data has been obtained bearing directly on the reaction of Rhamnus species to crown rust. It has been shown again that *R. frangula* is not immune from infection when inoculated with teliospores from *Avena sativa* and *Calamagrostis canadensis*. The development of pycnia was obtained on four different occasions. Infection is very dependent on the state of development of the leaf tissues and on the environmental conditions. It is quite conceivable that, if infection can be induced in the greenhouse, it also may be found under certain conditions in the open. It should be noted, however, that *R. frangula* is much more resistant than *R. cathartica* and *R. lanceolata*, although neither Klebahn (*7*), Eriksson (*5*), nor Mühlethaler (*10, 11*) noted any variation in the degree of susceptibility of the two first named species.

Up to the present writing, teliospores of *Puccinia coronata* from *Avena sativa*, *Calamagrostis canadensis*, *Festuca elatior*, and *Notholcus lanatus* have been applied as inoculum to species of Rhamnus. Infection on *R. frangula* has resulted only through teliospores from *A. sativa* and *C. canadensis*. None has developed through teliospores from *F. elatior* and *N. lanatus*, probably because of the fewer trials with spores from the two last mentioned hosts and the added difficulty of securing viable teliospores from Festuca and Notholcus.

Further evidence showing that the alternate-host range of the American crown rust differs from that found in Europe is apparent in the reaction of *Rhamnus dahurica*. Barclay describes a variety of *Puccinia coronata* as *P. coronata* var. *himalensis* on *Agrostis himalensis*. Later, Eriksson transferred this variety to *R. dahurica* and subsequently Dietel raised Barclay's variety to specific rank, naming it *P. himalensis*. Mühlethaler subsequently recognized this species, but suggested that it might be synonymous with *P. coronifera* Kleb. As shown in Table 1, this method of differentiation is questionable where teliospores from *Avena sativa* produced aecia on *R. dahurica*, which, in turn, was able to produce urediniospores on *A. sativa* (Table 5). These data show that *R. dahurica* can not act as a differential host for *P. himalensis* (Barcl.) Diet., since teliospores from *A. sativa* also can produce aecia on this alternate host.

Another very significant point bearing on the reaction of Rhamnus species to infection is the preference manifested by crown rust taken from different gramineous hosts. As shown in Table 1, *Puccinia coronata* from *Avena sativa* infects most readily *R. cathartica* and *R. lanceolata*. *R. alnifolia* is most susceptible to the Calamagrostis form taken from *C. canadensis*. However, in each case, different degrees of infection were obtained on at least 15 species. At the same time, *R. alnifolia* has consistently shown resistance to the *A. sativa* form. In the case of *R. caroliniana*, the differential reaction of the two sources of crown rust is even more marked. Teliospores from *A. sativa* gave normal infection, while those from *C. canadensis* showed only pycnial development.

Although the reaction of crown rust from all the gramineous hosts has not been fully studied up to the present writing, the data available indicate clearly that certain species of Rhamnus are markedly resistant to some and susceptible to others. In other words, a physiologic form has its alternate-host range as well as its gramineous host range. Clearly, then, when the reaction of additional physiologic forms has been studied, still further overlapping and extension of alternate-host ranges should be discovered. As shown earlier, crown rust from *Avena sativa* was transferred for the first time to *Berchemia scandens*, one of the Rhamnaceae.

An additional extension of the alternate-host range of crown rust developed when infection was obtained on *Lepargyrea canadensis of* the family Eleagnaceae through inoculation with teliospores from *Calamagrostis purpurascens*. It is not yet clearly understood just what alternate-host range and particular specialization that form of crown rust may have which produces abundant aecia on *Rhamnus purshiana*, a species indigenous to British Columbia, California, Oregon, Washington, and Idaho. The data here presented show the alternate-host specialization and the marked development of resistance and susceptibility of the physiologic forms Avenae and Calamagrostidis. These, combined with the extension of the alternate-host range beyond the genus Rhamnus and, in fact, outside the family Rhamnaceae, allow no alternative but to consider the crown-rust organism as one species with a wide alternate-host range. Crown rust, then, must remain as *Puccinia coronata* Corda.

Another point of much importance in connection with the rust reaction of Rhamnus is the influence exerted by different species of the host on the stability of the physiologic forms of the rust.

Among the European students of crown rust, Treboux alone, as noted earlier, presented results at variance with those of other workers. He obtained infection of grasses directly through aeciospores, while most of the other European investigators have sought to infect Rhamnus through teliospores of various grasses. Treboux (*12*, *13*) produced urediniospores on *Avena sativa* through inoculation with aeciospores from *R. frangula*. He also found that the aeciospores from *R. cathartica* infected *Agrostis stolonifera*, *Calamagrostis arundinacea*, and *Phalaris arundinacea*, all of which are listed as hosts of *Puccinia coronata* by Klebahn and Mühlethaler. On the other hand, in localities where only *R. frangula* occurs, two of the hosts of *P. coronifera*, namely, *A. alba* and *Poa pratensis*, were infected with *P. coronata*. Treboux took this to mean that specialization as reported by Klebahn and others probably did not exist. However, to the writer, Treboux's results, in connection with data here presented, suggest that the stability of the physiologic forms was changed through their culture on the Rhamnus hosts.

As shown in Table 5, teliospores from *Avena sativa* produced infection on eight species of Rhamnus. The aeciospores from each of these, in turn, caused abundant infection on *Notholcus lanatus* and *A. sativa*. This result is directly opposed to ordinary experience, for the form of crown rust on *N. lanatus* is highly specialized (*9*), only occasionally producing a subnormal infection on *A. sativa* when urediniospores are used as inoculum. Again, teliospores from *Calamagrostis canadensis* caused infection on *R. lanceolata*, these aeciospores producing urediniospores on *A. sativa* many times during a period of three years. It has been shown in an earlier paper (*9*) that the urediniospores on *C. canadensis* can only occasionally produce a subnormal infection on *A. sativa* and vice versa. On the other hand, teliospores from *A. sativa* produced aeciospores on *R. lanceolata* which produced urediniospores on *C. canadensis* (Table 5). This suggests that the physiologic-form relationship as expressed by the gramineous hosts may be altered by the Rhamnus host.

SUMMARY

The division of *Puccinia coronata* Corda into two species, as has been done by Klebahn, in Europe, is not justified in America.

The fact that *Rhamnus dahurica* produces aecia through teliospores from *Avena sativa* prevents this species of Rhamnus from functioning as a differential host for *Puccinia coronifera* Kleb. and *P. himalensis* (Barcl.) Diet., although Eriksson and Mühlethaler in Europe have claimed that it could so serve.

The alternate hosts of *Puccinia coronata* are not restricted to the genus Rhamnus or even to the family Rhamnaceae.

Thirteen species and one variety of Rhamnus, indigenous to the United States, and three species native to Europe, were investigated as possible alternate hosts of crown rust, from 1 to 28 times each, making a total of 364 trials. When *Rhamnus californica* var. *tomentella*, *R. caroliniana*, *R. cathartica*, *R. ilicifolia*, *R. lanceolata*, *R. pachyphylla*, *R. pinetorum*, *R. rubra*, and *R. smithii* were inoculated with teliospores from *Avena sativa*, the resulting infection was normal in at least one trial. *R. alnifolia*, *R. californica*, *R. crocea*, *R. dahurica*, and *R. tinctoria* also are susceptible, and may function

as alternate hosts of the Avenae form of *P. coronata*. *Rhamnus frangula*, *R. nevadensis*, and *R. purshiana* reacted with marked resistance to the physiologic form on *Avena sativa*.

Rhamnus alnifolia, *R. californica*, *R. crocea*, *R. lanceolata*, and *R. smithii* developed normal infection when inoculated with teliospores from *Calamagrostis canadensis*. It also was found that *R. californica* var. *tomentella*, *R. cathartica*, *R. pinetorum*, and *R. rubra* may function as alternate hosts of this physiologic form. The other eight species showed marked resistance.

Teliospores from *Festuca elatior* caused normal infection on *Rhamnus alnifolia*, *R. californica*, *R. cathartica*, and *R. lanceolata*. *R. californica* var. *tomentella*, *R. caroliniana*, *R. crocea*, *R. rubra*, and *R. smithii* produced a few aecia. Twelve trials on the seven remaining species showed that *R. ilicifolia* produced pycnia and *R. pachyphylla* developed flecks only.

Teliospores from *Notholcus lanatus* produced pycnia on *Rhamnus lanceolata*.

Ceanothus americanus, *Lepargyrea argentea*, and *Zizyphus lycioides* did not respond as alternate hosts of crown rust. *Berchemia scandens* was infected with teliospores from *Avena sativa*. *Lepargyrea canadensis* produced aecia when exposed to infection with teliospores from *Calamagrostis purpurascens*.

Rhamnus species, functioning as alternate hosts, may alter the physiologic response of specialized forms.

A total of 1,021 plantings of *Rhamnus cathartica* were found in the upper Mississippi Valley. Of these, 282 were rural and 739 urban, with a total of 93,041 bushes, besides 44,395 feet of buckthorn hedge of uncounted bushes. In addition, many areas of escaped plants were located in Illinois, Montana, and Wisconsin.

During the past nine years in Iowa, aecial infection has appeared on *Rhamnus cathartica* and *R. lanceolata* previous to the development of uredinia on *Avena sativa*. These two species of Rhamnus have been instrumental in starting local and general epidemics in Iowa within the past two years.

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